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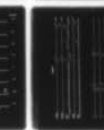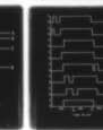1972   S W STROPES, D HUNSAKER, L C JOHNSON

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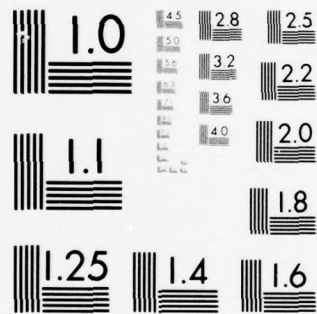
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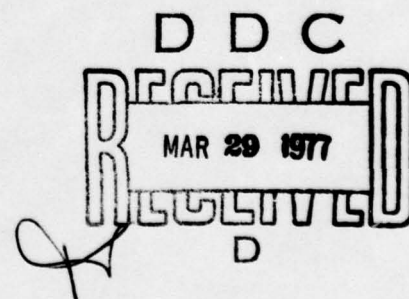
ELECTROGRAPHIC AND BEHAVIORAL CORRELATES OF
SLEEP IN THE FRINGE-TOED LIZARD, UMA NOTATA

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NAVAL MEDICAL RESEARCH AND DEVELOPMENT COMMAND

BETHESDA, MARYLAND

ELECTROGRAPHIC AND BEHAVIORAL CORRELATES OF SLEEP IN THE FRINGE-
TOED LIZARD, UMA NOTATA

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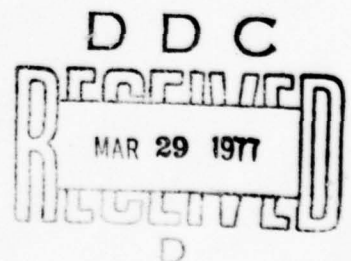California.

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EEG AND SLEEP BEHAVIOR IN THE LIZARD

ABSTRACT

Behavioral and electrographic aspects of sleep in Uma notata were investigated. These burrowing lizards slept during the presence and absence of sand, under conditions of constant light and temperature (37 ± 1 C).

When sand was present, most of their sleep behavior occurred while burrowed. Under constant light and temperature, burrowing continued, but was arrhythmic. While exposed to an 8-hr light, 16-hr dark photoperiod (temperature remaining constant), a rhythmicity in burrowing periodicity developed, in all lizards, after 7 days. The animals burrowed in relation to the termination of the light cycle. Light appeared to be a prime exogenous mechanism regulating an internal biological clock in these lizards.

These lizards exhibited two distinct patterns of electroencephalograms during sleep. A high-voltage, slow-wave electroencephalogram alternated with a lower voltage, faster frequency wave form. The low-voltage desynchronized EEG sleep pattern occupied 31% of the total sleep time. Eye-movement bursts of brief duration were generally accompanied by the low-voltage, fast-wave EEG. While burrowed, 5.7% of the total sleep time was occupied by eye movements. No change in neck muscle tonus was observed during sleep.

INDEX TERMS: Sleep; Lizard (Uma notata)

INTRODUCTION

The purpose of this study was to investigate sleep behavior in the Colorado Desert fringe-toed lizard, Uma notata. In reptiles, the presence of sleep is not obvious. Allison and Van Twyver (1970) stated that reptiles possess only rudiments of sleep compared to mammals. They observed that in both amphibians and reptiles, there are quiet and immobile periods but the animal is still essentially awake. Berger (1969) reported that the presence of nonconjugate eye movements and periods of behavioral unresponsiveness are insufficient criteria for the definition of sleep. These equivocal sleep findings led Snyder (1966) and Allison and Van Twyver (1970) to propose that sleep evolved with the evolution of homeothermy and that the need for sleep is a consequence of the ability to regulate body temperature. Sleep, thus, possibly serves to reduce metabolism when energy expenditure is not desirable.

Where reptilian sleep has been reported, the presence of both rapid eye movement (REM) sleep and slow-wave sleep (SWS) have not been consistently found. Nonconjugate REM periods were observed in the chameleon, Cameleo melleri, by Tauber, Roffwarg, and Weitzman (1966); however, electroencephalographic (EEG) desynchronization and electromyographic (EMG) hypotonia did not occur during these periods (Berger, 1969). REM sleep was not observed in either the tortoise (Hermann, Jouvet, and Klein, 1964) or the Caiman sclerops (Rechtschaffen, Bassan, and Ledecky-Janecek, 1968). Peyrethon and Dusan-Peyrethon (1969) studied a representative (python, caiman, and turtle) of each of the three major reptilian orders and reported that each showed SWS but no clear indications of REM sleep were found.

Uma notata was selected for the present investigation because of its behavior relating to sleep and its excellence as a laboratory animal. This lizard periodically burrows beneath the sand with the eyes closed and the body relaxed and immobile, presumably undergoing sleep behavior. This sleep-like behavior has also been observed while Uma is on the sand surface.

METHOD AND MATERIAL

Experimental Animals

Eleven lizards, 7 males and 4 females, were used during the experiments. Nine were adults (snout-vent over 80 mm) while two were immature (snout-vent over 70 mm). The lizards were maintained in a plywood box 122 cm X 46 cm X 46 cm. The floor of the box was covered with 4 cm of sand, collected from the capture site. Temperature was controlled by infrared lamps suspended above the cages.

A 200-watt light bulb, at one end of the enclosure, provided a thermal gradient. The light was controlled by an automatic timer which operated on an 8-hr light, 16-hr dark cycle. The light turned on at 9 AM and off at 5 PM.

The lizards were fed meal worms ad libitum throughout the experiment. All animals ate well and required no drinking water under these conditions.

Experimental Design

The study was divided into three experiments: In Experiment 1, both the general and burrowing activity of Uma notata and the effect of the absence of sand on sleep behavior were observed. These observations were made under constant light and temperature conditions. Experiment 2 investigated the rhythmic burrowing

activity of Uma under a photoperiod, while at constant temperature.
In Experiment 3, lizards were monitored electrographically to deter-
mine whether the electrophysiological signs of sleep were present.
Comparisons were made of the general sleeping behavior in Experi-
ments 1 and 2, to that seen in Experiment 3, and the electrographic
recordings during this sleeping behavior.

Experiment 1

Eight lizards were individually enclosed in plastic containers,
32 cm high and 24 cm in diameter at the base. Sand surface temper-
atures were recorded during each observation session, and ranged
from 36-38 C. Temperatures were obtained with a "banjo-tip" therm-
istor attached to a Yellow Springs tele-thermometer. Two 200-watt
light bulbs, suspended 61 cm above the containers, supplied the
light source.

The lizards remained in the experimental setup 4 days prior to
the recording periods. To determine the sleep and burrowing pat-
terns, the lizards were observed 8 hrs a day, at 10-min intervals,
for 12 days. Recording sessions were separated into three 8-hr
shifts; (1) from 3 AM to 11 AM, (2) 11 AM to 7 PM, and (3) 7 PM to
3 AM. Every 3 days of observation constituted a 24-hr day. Follow-
ing the 12 days of observations with sand, the sand was removed and
the observations were continued for 3 more days. This shorter
recording time prevented any serious loss of burrowing activity or
periodicity which may have occurred under prolonged sandless condi-
tions.

Four general types of behavior were recorded: (1) active
waking (eyes open), (2) resting (eyes closed) with a response (eye

opening) to a puff of air directed toward the head region, (3)
sleeping (eyes closed) with no observable response (eyes remaining
closed) to a puff of air, and (4) burrowed (head completely covered
with sand). The air puffs were delivered from a plastic water
bottle with an attached plastic nozzle. The nozzle was pointed at
the lizard and quickly, but uniformly, squeezed, providing a 1/2-
sec duration puff.

Experiment 2

Eight lizards, five from Experiment 1 plus three reserve spec-
imens, were observed under the same conditions of Experiment 1 with
sand, except the light was set on a cycle of 8 hrs light, 16 hrs
darkness. The timer-controlled light cycle began at 9 AM and ter-
minated at 5 PM. Infrared heat lamps, controlling the temperature,
emitted dim light during the "dark" part of the cycle, so the
lizards were not in total darkness. The lizards were observed for
7 days.

Experiment 3

Two Uma were randomly selected from the lizards used in Exper-
iment 1, and two were selected from the ones used in Experiment 2.
Each of these four lizards was used for continuous EEG monitoring
during a 24-hr period. Five were used for shorter periods of sleep
recordings.

Each lizard was implanted with seven electrodes (Fig. 1).
Each electrode was a platinum-coated silver wire lacquered within 2
mm of the tip. The electrodes were attached to flexible, insulated
wires, approximately 13.5 cm in length, which were connected to a
flat junction box. With the exception of the EEG electrode, the 2

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Insert Fig. 1 about here

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mm bare tips were bent into a U shape and attached to the lizard
subcutaneously. The implanted electrodes were secured to the
animal by either Eastman 310 cement, or a glue formula containing
ether, ethanol, and parlodion. The junction box was taped to the
posterior dorsal back region of the lizard by human electrode tape.
The electrode placement and potentials measured were: (A) at the
junction of the right eyelid and skull, electrooculogram (EOG);
(B) at the junction of the left eyelid and skull (EOG); (C) dorsal
posterior region of the skull, reference electrode; (D) brain,
(EEG); an electrode was inserted through the parietal eye opening
in the skull, and situated on or near the cerebral hemispheres in
the telencephalon; (E) dorsal neck muscles, (EMG); (F) dorsal
region of the back, ground electrode; and (G) mid-dorsal back
region, electrocardiogram (EKG). Each lizard was anesthetized with
ether for implantation.

After implantation, the lizards were observed for 3 days prior
to recordings. This was sufficient time to allow for surgical
recovery. All animals continued to eat, burrow, and showed no
signs of behavioral irregularity or restriction due to the elec-
trodes.

The implanted lizards were transported in their individual con-
tainers from San Diego State University to the Neuropsychiatric
Research Laboratory at the Naval Hospital, San Diego, for EEG moni-
toring using a 12-channel Beckman dynograph. The conditions

existing during Experiments 1 and 2 were duplicated at the hospital.
Lizards from these experiments were maintained at temperatures
ranging from 36-38 C. Lizards from Experiment 1 were under con-
stant light, while those from Experiment 2 were under 8 hrs light,
16 hrs darkness. Sand was present for each lizard. After a 24-hr
acclimation period at the hospital, each lizard was connected to a
flexible standard clinical EEG electrode cable, attached to the
junction box on the animal's back. Observations revealed no sig-
nificant restriction of lizard movement due to this equipment
attachment.

RESULTS

Experiment 1

In the presence of sand, these eight lizards spent very little
time asleep on the surface (see Table 1). The mean percent of time
spent sleeping (while visible) was significantly higher without
sand than with sand (t-test for correlated means $P < 0.05$). When
burrowed time was included, however, the total amount of sleep
behavior was significantly higher ($P < 0.01$) with sand than without
sand. Absence of sand also significantly increased ($P < 0.01$) the
surface resting time, but the difference in percent of time actively
awake was not significant between the sand and sandless conditions.

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Insert Table 1 about here

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While exposed to constant light and temperature, there was no
evidence of a regular pattern for resting or sleeping on the sur-
face or of burrowing rhythmicity in any of the lizards.

Experiment 2

The effect of a photoperiod under constant temperature conditions, on the burrowing habits, is illustrated in Fig. 2. Lizards #2, #4, and #6 through #11 were used. For this study, all animals were shifted from a constant light condition to a light cycle.

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Insert Fig. 2 about here

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After a period of 7 days, a trend in the pattern of burrowing rhythmicity was evident in all lizards. They all appeared to burrow in relation to the termination phase of photoperiod, rather than the beginning.

Experiment 3

As in Experiments 1 and 2, sleep was behaviorally defined when the surfaced animal was lying head down, eyes closed, body relaxed, with legs spread outward, and showed no observable response to an air puff. When burrowed (head completely under the sand), sleep onset was defined by a decrease in heart rate and change in EEG pattern similar to that seen in the sleeping surfaced lizards. Eye movements during awake and asleep were visually observed when the animal was on the surface, for correlation with the polygraph write-out (see Fig. 3).

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Wakefulness

During active waking, the EEG was composed of large amplitude

(50-100 µV) slow waves (1-4 Hz), mixed with lower amplitude wave
forms, generally in the range of 6-9 Hz, with an amplitude of 30-50
µV (see Fig. 3). These wave forms were sometimes masked and oblit-
erated by electrode sway artifacts, high-voltage electrical poten-
tials overriding and distorting the record. Some of the awake
high-voltage activity were also generated by massive eye, neck, and
body movements typical in this active lizard. Some of the faster
low-voltage activity in the awake EEG were undoubtedly muscle poten-
tials. This waking EEG activity correlates well with Hunsaker's
and Lansing's (1962) findings of EEG studies in Sceloporus.

Sleep

The EEG during sleep was of lower voltage than that seen
during waking, and was similar whether the lizard was burrowed or
asleep on the surface. Typically, the sleep EEG consisted of
relatively high-voltage, slow-wave periods alternating with periods
of desynchronized activity of lower voltage, faster waves. The
slow waves were characteristically in a range of 1-4 Hz, mean of 2
Hz, with an amplitude of 15-75 µV, mean of 30 µV. These slow waves
were, in most instances, rhythmic spike-like potentials occurring
on a low-amplitude background. SWS, though often irregular in
appearance, was quite distinct from desynchronized fast-wave sleep.
The low-voltage, desynchronized EEG was characterized by a wave
form of 5-8 Hz, with an amplitude of 10-30 µV. Occasionally, high-
voltage spike potentials would appear in the low-voltage record.
These spikes were generally between 40-60 µV in amplitude. The
transition from slow to the relative fast-wave sleep (and vice
versa) was rapid, usually less than 3 sec. Figure 4 illustrates

representative sleep patterns in three Uma.

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Insert Fig. 4 about here

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Nonconjugate eye-movement bursts were observed in all animals recorded. Eye movements of two or more sec in duration were considered an eye-movement burst. In a series of 371 such bursts, the duration ranged from 2-160 sec. The majority (207) were in the 2.5-10.0 sec range with some bursts (47) up to 30 sec in length.

In all lizards, eye movements accompanied episodes of low-amplitude, relative fast-wave EEG from 55-95% (mean 75%) of the time, and accompanied the higher amplitude, slow-wave EEG 5-45% (mean 25%) of the time. This difference was significant using the Wilcoxon signed rank test (P < 0.05). Eye-movement bursts, however, comprised only 3.8-7.9% (mean 5.7%) of the total sleep time for individual sleep records. Figure 4 shows an eye-movement burst during fast-wave sleep. In lizards #1 and #10, there were eye movements during SWS.

SWS generally dominated the first 5 min of the sleep record. After this initial period, the slow waves alternated with the faster waves during the entire sleep period. Of the four lizards monitored, the percent of desynchronized relative fast-wave periods ranged from 29-34% (mean of 31%), while slow waves occupied 66-72% (mean of 69%) of the record (Fig. 5).

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Insert Fig. 5 about here

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Heart Rate

Heart rate varied during different activities. An active, vigilant lizard usually had a heart rate of 90-110 beats per minute (bpm). A resting or sleeping animal, on the sand surface, had a heart rate between 50-80 bpm. Immediately subsequent to burrowing, the heart rate ranged from 87-103 bpm, but rapidly decreased with sleep onset and remained in the range of 40-60 bpm (mean 47 bpm) throughout the remainder of the sleep period. While the heart rate tended to be faster during fast-wave sleep, the difference from SWS was not significant.

The muscle tonus did not significantly change in amplitude between periods of resting, waking, and sleep. The only noticeable variation was observed when the electromyogram (EMG) of a vigilant or motile lizard was compared to a sleeping one. Even during these periods, the difference was slight. The differences were assumed to be a function of the neck muscles used to elevate the head during wakeful periods.

DISCUSSION

In nature, Uma notata spends much of its time buried beneath the sand. This lizard is generally active during early morning and late afternoon, while inactive (burrowed) at night and midday. Some of the reasons attributed to burrowing behavior, in Uma, include: flight from predation (Stebbins, 1944), escape from excessive environmental temperatures (Stebbins, 1944), regulation of evaporative water loss (Deavers, 1969), feeding (Carpenter, 1963), and sleep (Regal, 1967).

In the laboratory, these lizards spent significantly more time

resting and sleeping while visible during the absence of sand than with sand. Without sand, the lizards were deprived of their preferred sleep medium and thus were forced to sleep in an unnatural situation, but, since they still needed to obtain sleep and rest, a higher percentage of surface sleep was expected.

The lizards, under constant light and temperature, were burrowed 39% of a 24-hr day. There was, however, no indication of a regular burrowing rhythmicity, suggesting that changes in light or temperature may control burrowing patterns in Uma. Enright (1970) stated that many organisms may have an endogenous rhythmicity which depends on entrainment by day-night cycles of light or temperature. Brown (1959) indicated that an animal may alter or shift such a rhythm under constant conditions. He termed this shifting as "autophasing." With the lack of an external entrainment force, the cue necessary to trigger an internal clock may be absent. Uma notata appears to be lacking such a cue for periodic sleep to occur under constant light and temperature.

Supporting the importance of external cues, in Experiment 2, lizards exposed to a photoperiod demonstrated a rhythmicity of burrowing after a period of 7 days. In the field, a thermoregulatory response to excessive temperatures may cause Uma to burrow during the day; however, a photoperiod would seem to be a logical mechanism for regulating inactivity and sleep in a diurnal lizard at night.

Uma notata exhibited the behavioral requisites for sleep during both the presence and absence of sand. These animals, when sleeping (and resting), were typically relaxed and immobile, with

the head down, eyes closed, and legs spread outward. When a lizard

was observed sleeping (no response to an air puff), it usually

would not respond to taps on the container, excessive air puffs, or

loud noises. Heart rate was invariably slowed when these behavioral

characteristics of sleep were present.

The appearance of eye movements and two distinct phases of

EEGs were characteristic electrographic correlates of behavioral

signs of sleep in Uma notata. These results present clear evidence

of the existence of a cyclically recurring EEG pattern during sleep

in this reptile. Because the eye movements of the Uma do not show

the speed and burst organization of rapid eye movements seen in

mammals, we have refrained from calling these eye movements REMs,

but the general appearance of eye-movement bursts, accompanied by

the desynchronized relative fast frequency EEG, suggests that the

mechanisms of Uma sleep are related to those of the REM and NREM

sleep patterns found in the higher classes of vertebrates. The

finding that this lizard does show eye movements during SWS, and an

apparent lack of any change in muscle tonus when changing types of

sleep, suggests that sleep cycles, though evident, are nonetheless

somewhat primitive.

Electrographically, Uma sleep appears to be more advanced than

fish, amphibians, and other reptiles investigated to date. Tauber

and Weitzman (1969) found REMs during inactive periods in Bermuda

reef fish; however, none of the other electrographic requisites for

sleep were observed. Hobson, Goin, and Goin (1968a,b) stated that

the bullfrog (Rana catesbeiana) does not sleep, while the tree frog

(Hyla septentrionalis) exhibited no change in EMG, or showed ocular

movements during sleep, "though their resting behavior more clearly resembles sleep than does that of bullfrogs." Lucas, Sterman, and McGinty (1969) found no evidence of REM sleep in the salamander (Ambystoma tigrinum) although "EEG samples from quiet vs. active salamanders showed frequent changes similar to those observed in homologous mammalian neural tissue, thus suggesting the existence of the primordium of sleep and wakefulness in this primitive verte-brate." REM sleep was not observed in the turtle (Klein, 1963) or the caiman (Rechtschaffen et al., 1968). Tauber et al. (1966) did find REM periods occurring in the chameleon, Cameleo melleri. Although the EEG showed obvious differences between waking and sleep stages in the chameleon, no change in the basic sleep EEG pattern was seen to occur during the presence of REM periods.

The progressive evolutionary trend in sleep from amphibians through mammals has raised questions as to the evolutionary signif-icance of the various findings. Klein, Michel, and Jouvet (1964) have reported two types of sleep in the chicken, and Walker and Berger (1972), as well as Van Twyver and Allison (1972), have reported that REM sleep occupies about 7% of the total sleep time in the pigeon. In their 1972 paper, Van Twyver and Allison noted, "Since PS [paradoxical sleep] is present in birds, it also has either evolved twice, once in therian mammals and once in birds, or else it was present in the early reptiles from which forms ances-tral to both mammals and birds arose." Since PS was not found in the echidna, they reasoned the most likely alternative was that PS evolved twice, i.e. independently in birds and mammals. They also postulated that SWS also evolved independently in birds and mammals.

Our finding of clear indications of SWS and a type of REM sleep in
Uma offers some support to the hypothesis that PS is present in at
least some reptiles and may be a part of a common evolutionary
pattern. Perhaps the echidna is an exception in this evolutionary
progression, or some form of REM or REM-like sleep will be found in
subsequent studies with the echidna.

Allison and Van Twyver (1970) maintained that an animal's food
getting habits and the security of its sleeping arrangements deter-
mine if it is a "good" or "poor" sleeper. A "good" sleeper would
be an animal with long sleep periods and a high percentage of "deep"
or REM sleep. Predators such as the cat, dog, and man are "good"
sleepers, since they generally are not preyed upon. Prey species
such as goats, guinea pigs, donkeys, sheep, and rabbits are "poor"
sleepers. They have short sleep periods, with very little REM
sleep. However, prey species which have secure sleeping arrange-
ments (mole, ground squirrel, macaque, and chimpanzee) generally
are "good" sleepers with high amounts of REM sleep (Allison and Van
Twyver, 1970). Uma appears to be a "good" sleeper. In the field,
these lizards burrow during the night and often during midday.
While burrowed, the lizard is afforded extended sleep periods
because of its relatively safe sleeping arrangement. An average of
31% of its total sleep is occupied by desynchronized EEG activity
with eye movements. Only additional studies from this lizard and
other reptiles will determine whether this REM-like state in Uma is
the precursor of the REM sleep seen in higher vertebrates.

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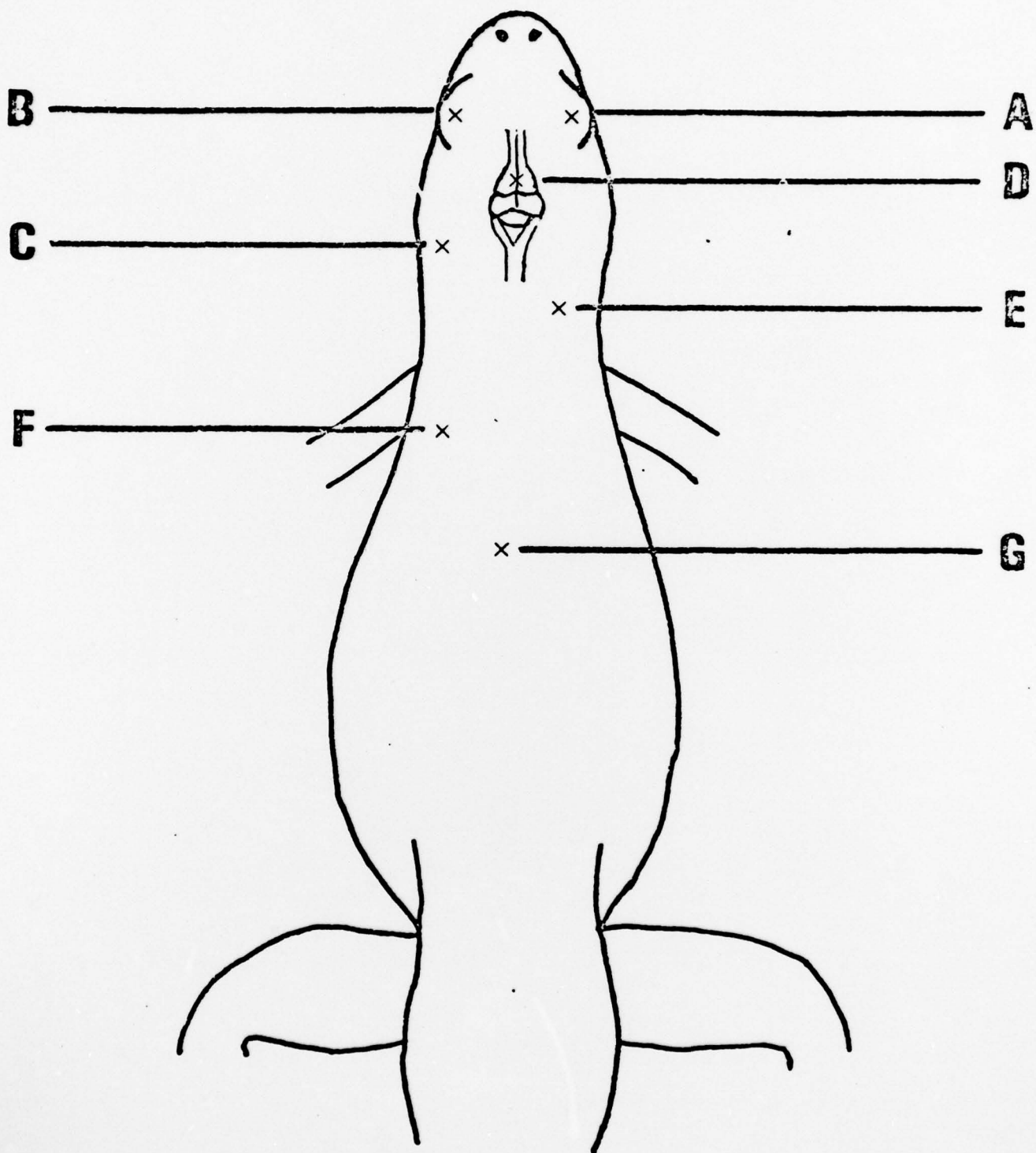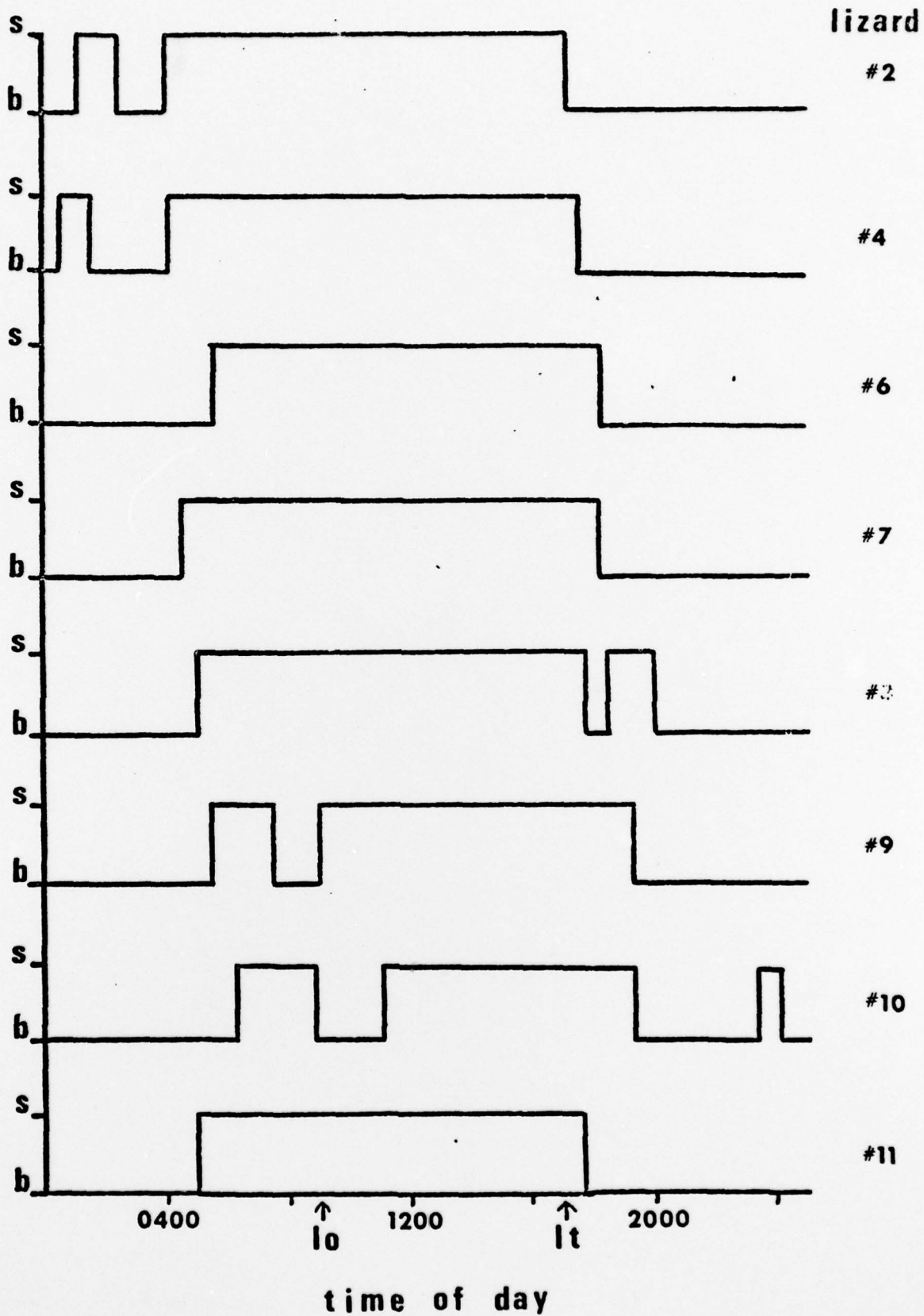   pigeon (Columba livia). Beh. Biol. 7, 195-203.

TABLE 1

Percent of time each activity was recorded during Experiment 1, with sand and without sand (numbers in parentheses). Recording sessions A, B, and C were combined to obtain these data.

	Activity			
Lizard	Burrowed (%)	Surface resting (%)	Surface sleeping (%)	Surface waking (%)
1	59	10 (33)	0 (11)	31 (56)
2	44	15 (32)	2 (21)	39 (47)
3	7	6 (24)	1 (1)	86 (75)
4	29	30 (49)	4 (2)	37 (49)
5	55	22 (25)	9 (31)	14 (44)
6	35	19 (42)	2 (21)	44 (37)
7	23	24 (55)	2 (9)	51 (36)
8	60	20 (30)	7 (5)	13 (65)
Mean	39	18 (36)	4 (13)	39 (51)

LEGENDS FOR FIGURES

Fig. 1.   Location of implanted electrodes. A and B - right and
left (EOG); C - base of skull (ref); D - brain (EEG); E -
neck (EMG); F - back (gnd); G - back (EKG).

Fig. 2.   Burrowing rhythmicity during a 24-hr photoperiod on 7th
day of observation (b - burrowed; s - surfaced; lo - light
on; lt - light terminated).

Fig. 3.   Bursts of visually observed eye movements during active
waking, eyes open, period, A, B, C. The eye movements of
burst B were in response to knocking on side of container.
The heart rate varied from 84 to 96 during this awake
period. L - left, and R - right.

Fig. 4.   Periods of slow-wave sleep (SWS) and fast-wave sleep (FWS)
in three lizards. The calibrations for lizard #1 were the
same as those for lizard #5. The EEG and EMG calibration
was the same for all lizards. There is no change in EMG
as the lizard enters or leaves FWS. The average heart
rate for lizard #5 was 38 bpm; for lizard #1, 42 bpm; and
for lizard #10, 48 bpm.

Fig. 5.   Percent of low voltage, fast frequency sleep per 10-min
interval (inclusive) during burrowed sleeping period.
Vertical bars represent amount of eye movements during
each interval; dark part of bars - amount of fast EEG
accompanying eye movements; light part of bars - amount of
slow EEG accompanying eye movements; digits indicate the
number of eye movement periods in each interval.

B ——————————— A
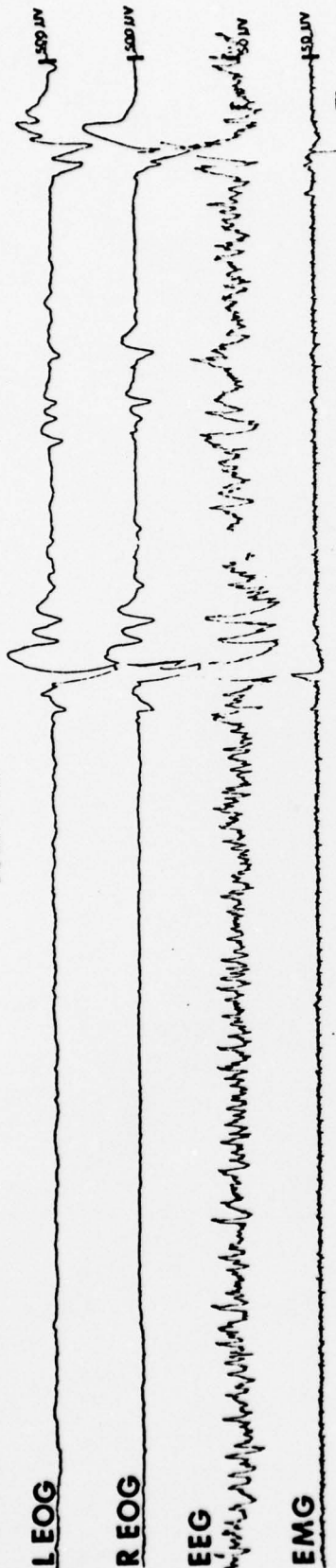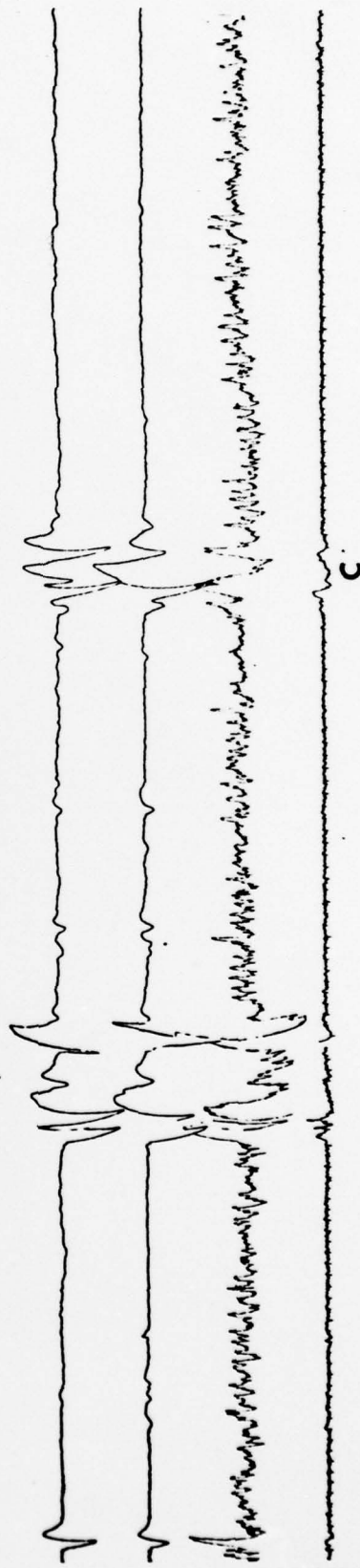
D

C ——————————— E

F

G

time of day

AWAKE

L EOG

R EOG

EEG

EMG

EKG

LEOG

REOG

EEG

EMG

EKG

EEG

LIZARD 5

SWS FWS SWS

50 μV
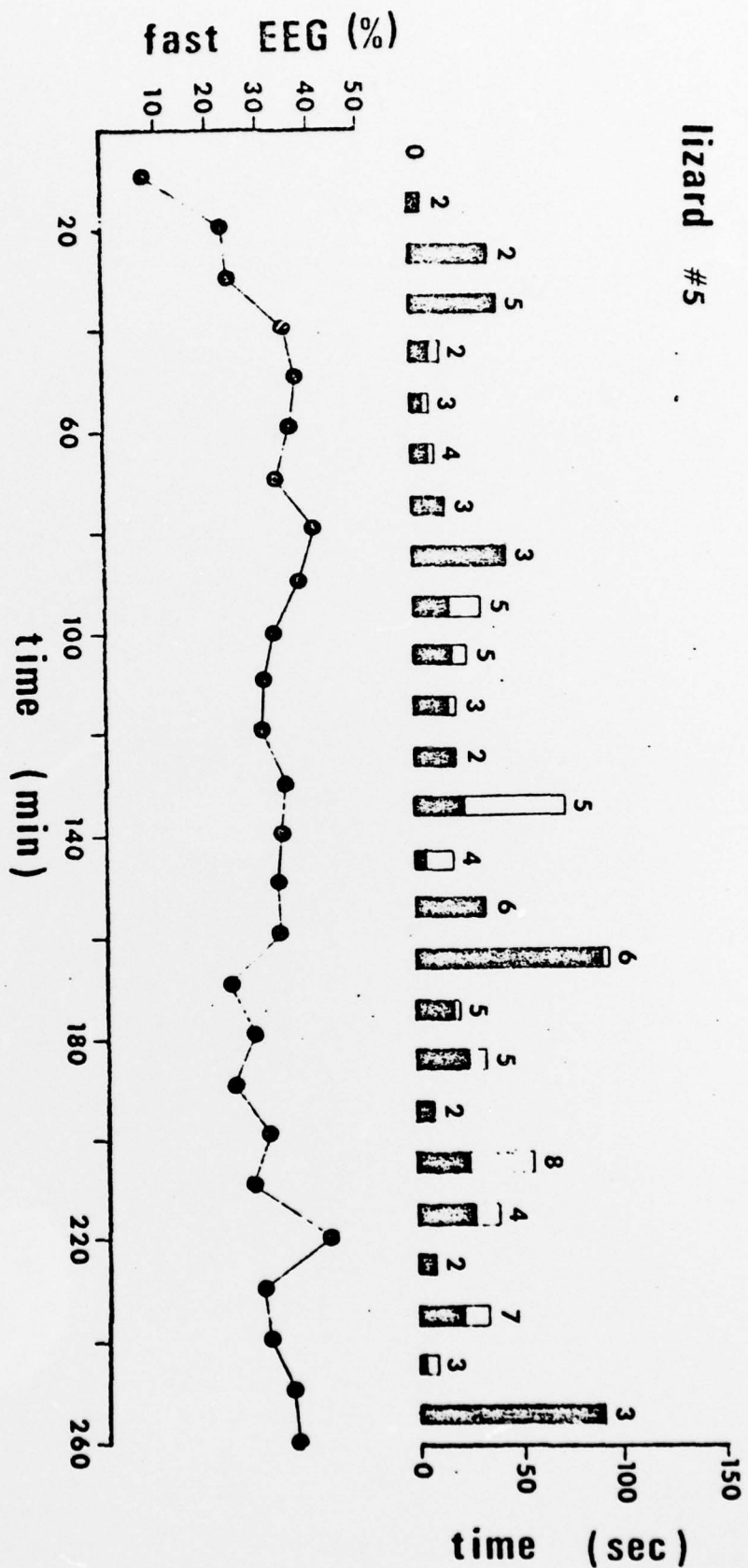
50 μV

100 μV

500 μV

1 SEC

LIZARD 1

SWS FWS SWS

SWS FWS SWS

250 μV

250 μV

LIZARD 10

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Sleep
Lizard (Uma notata)

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

Behavioral and electrographic aspects of sleep in Uma notata were investigated. These burrowing lizards slept during the presence and absence of sand, under conditions of constant light and temperature (37 ± 1 C).

When sand was present, most of their sleep behavior occurred while burrowed. Under constant light and temperature, burrowing continued, but was arrhythmic. While exposed to an 8-hr light, 16-hr dark photoperiod (temperature remaining constant), a rhythmicity in burrowing periodicity developed, in all lizards, after 7 days. The animals burrowed in relation to the termination of the light

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cycle. Light appeared to be a prime exogenous mechanism regulating an internal biological clock in these lizards.

These lizards exhibited two distinct patterns of electroencephalograms during sleep. A high-voltage, slow-wave electroencephalogram alternated with a lower voltage, faster frequency wave form. The low-voltage desynchronized EEG sleep pattern occupied 31% of the total sleep time. Eye movement bursts of brief duration were generally accompanied by the low voltage, fast-wave EEG. While burrowed, 5.7% of the total sleep time was occupied by eye movements. No change in neck muscle tonus was observed during sleep.